**Bulletin, Southern California Academy of Sciences**

VOLUME 58 - - - - - - - - - PART 3, 1959

# *TAPOCHOERUS*, A UINTAN DICHOBUNID ARTIODACTYL FROM THE SESPE FORMATION OF CALIFORNIA

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(A contribution from the University of California Museum of Paleontology)

ABSTRACT

*Hyopsodus egressus* Stock, 1934b, from the Uintan (late Eocene) Tapo Ranch faunule, Sespe formation, Southern California, is not a hyopsodont condylarth. The species is here made the type of *Tapochoerus*, new genus, a dichobunid artiodactyl. A hypocone and non-hypertrophied metaconule on the upper molars and the lack of a metaconid on $P_3$, combined with presence of a metaconid on $P_4$, a paraconid on $M_1$ and $M_2$, and the nature of the lower molar hypoconulids, indicate affinity with the most primitive members of the dichobunid subfamily Homacodontinae. The recently proposed dichobunid subfamily Antiacodontinae Gazin, 1958, is rejected and its members returned to the Homacodontinae.

Among the fossil mammal remains collected by the California Institute of Technology at Locality 180 on the Tapo Ranch in Simi Valley, Southern California, are half a dozen jaws and more than a dozen teeth of a Uintan (late Eocene) mammal which Chester Stock (1934b) named as a new species of the condylarth genus *Hyopsodus*, *H. egressus*. In his paper Stock did not make comparisons with remains of any dichobunid artiodactyl. Recent clarifications of dichobunid interrelationships by C. L. Gazin (1952, 1955, 1958) have made it increasingly apparent to the author that *Hyopsodus egressus* Stock, 1934b, is not a hyopsodont condylarth but rather is a dichobunid artiodactyl related to *Microsus, Hexacodus, Antiacodon, and Auxontodon*. *"H." egressus* possesses a combination of characters which indicates that it represents a Uintan member of a primitive homacodont dichobunid lineage that may have been isolated in California west of Mohavia throughout most of the Eocene. By Uintan time the lineage had become generically distinct from its closest dichobunid allies.

I wish to thank Drs. D. E. Savage and C. L. Gazin and Mr. W. A. Clemens for reading the manuscript and for criticism. Dr. Theodore Downs and Mr. William Otto were also of considerable assistance. The illustrations were drawn by Howard Hamman (Plate 37, fig. a, c) and Owen J. Poe (Plate 37, fig. b.).

### FAMILY DICHOBUNIDAE GILL, 1872

### SUBFAMILY HOMACODONTINAE PETERSON, 1919a

### *Tapochoerus*, NEW GENUS

ETYMOLOGY: TAPO, Tapo Ranch, Simi Valley, Southern California; *choerus*, Gr. *choiros*, pig, with reference to the bunodont dentition.

TYPE: *Hyopsodus egressus* Stock, 1934b.

TYPE OF *H. Egressus:* Calif. Inst. Technology[1]. No. 1590, fragmentary right lower jaw with $P_4$ - $M_3$, figured by Stock, 1934b, Plate I, figs. 3, 3a.

PARATYPES OF *H. egressus:* Calif. Inst. Technology Nos. 1596, left $M^3$, 1597, right $M^1$ or $M^2$, and 1598, right $M^1$ or $M^2$. Paratypes figured by Stock, 1943b, Plate I, figs 4, 5, and 6, respectively. C. I. T. No. 1598 refigured, this paper, fig. 1, b.

HYPODIGM: Type, paratypes, and the following specimens: C.I.T. Nos. 1292, two sections of a right lower jaw with $M_2$ - $M_3$, $P_3$ - $P_4$, and roots of $P_2$, figured by Stock, 1934b, Plate I, figs. 7, 7a, 7b, 7c; 1587, fragmentary right lower jaw with $M_1$ - $M_3$; 1588, fragmentary right lower jaw with $P_4$ - $M_2$, this paper, fig. 1, c; 1589, fragmentary left lower jaw with $M_1$ - $M_3$; 5224, fragmentary right lower jaw with two molars; 5225, right $M^3$; 5226, right $M^1$ or $M^2$; 5227, right $M^3$; 5228, ½ upper molar; 5229, fragmentary left upper molar; 5230, associated left ?$M^2$ and $M^3$, this paper, fig. 1, a; 5231, left lower molar; 5232, left lower molar; 5233, anterior, caniniform tooth, probably from the upper dentition and probably this species, though this is not proven; 5234, left $P_4$.

TYPE LOCALITY OF *Tapocherus egressus:* Tapo Ranch, Calif. Inst. Technology Locality 180, Uintan part of Sespe formation, progressive grid coordinates 1,227,475 - 1,250,500, elevation 1425 feet m. s. l., Santa Susana Quadrangle (1943; 1:62,500), north side of Simi Valley, Ventura County, California.

AGE: Late Uintan (approximately "Uinta C"), assigned to late Eocene.

DISTRIBUTION: Type Locality only.

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[1]. All fossil mammal specimens formerly in the collections of the California Institute of Technology are now the property of the Los Angeles County Museum.

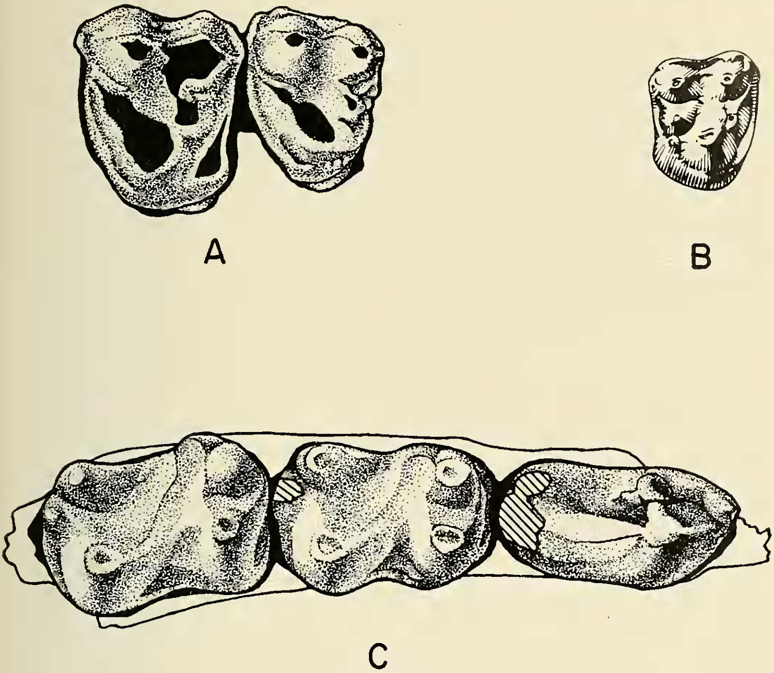


PLATE 37

*Tapochoerus egressus* (Stock, 1934b). A: C. I. T. No. 5230, associated left ?$M^2$ and $M^3$, x3. B: C. I. T. No. 1598, right ?$M^2$ (Stock, 1934b, PlateI, fig. 6. Photograph poorly retouched in region of hypocone), x2. C: C. I. T. No. 1588, right lower jaw fragment with $P_4 - M_2$, x3. A and C, by Howard Hamman; B by Owen J. Poe.

GENERIC DIAGNOSIS: Primitive dichobunid artiodactyl in which the teeth are more bunodont than selenodont; the hypocone is retained on $M^1$ and/or $M^2$, the metaconules are large but are neither hypertrophied nor markedly displaced and, when unworn, possess five posterior crests; there is neither a mesostyle nor ectoloph ribbing on $M^1$ and/or $M^2$, strong diastemata isolate the double-rooted $P_2$; $P_3$ is trenchant and lacks a metaconid; $P_4$ is also trenchant but possesses a distinct entoconid and a metaconid which separates from the protoconid high on the crown; $M_1$ has a strong paraconid separated from the metaconid but not as widely separated as in *Antiacodon* or *Auxontodon*, $M_2$ has a variably separated paraconid, and $M_3$ has a fused single lingual trigonid cusp; all the lower molars are elongate, with hypoconulids closely similar to those of *Hexacodus*.

Revised Diagnosis and Description of Tapochoerus Egressus

$M^1$ and/or $M^2$ with high, conical paracone possessing anterior and posterior crests, a basal connection to the weak posterior wing of the protoconule, and slight fluting labially in the area where the labial cingulum is interrupted; metacone also with anterior and posterior crests, but without marked basal connection to metaconule; protocone conical, but connected to protoconule by strong ridge; protoconule strong, with strong anterolabial wing to anterior cingulum at base of paracone and very weak labially directed posterior wing joining small basal projection from paracone; metaconule very strong, conical, and with a weak anterolabial wing, a moderately strong posterolabial wing terminating anterolingual to the metastyle, and four additional flutings or minor crests placed diagonally on the posterior slope; the most lingual of these accessory crests faces a cuspule on the posterior cingulum labial to the hypocone; almost the whole circumference of the tooth bears a robust and crenulated cingulum which is interrupted only briefly at the labial base of the paracone (where there is generally a small notch just posterior to the interruption) and at the lingual base of the protocone, but even these gaps are filled with small crenulations at the proper site; the hypocone is merely a moderately large cuspule on the cingulum and does not approach the size of the metaconule, though the cusp is at least present, in contrast to members of the Helohyinae and Diacodexinae. (See Sinclair (1914a, p. 290, etc.). Gazin (1952, p. 73) mentions a hypocone in some molars referred to *Bunophorus*, stating that the cusp is approximately equivalent in size to the protoconule and metaconule.).

$M^3$ triangular, with high, conical paracone and smaller metacone linked by crests forming a stronger ectoloph than that of $M^1$ and/or $M^2$; an incipient mesostylar rib strengthens the ectoloph at its mid-point; the protocone is approximately the size of the metacone and is linked to the protoconule as in $M^1$ and/or $M^2$; the protoconule is as in the other molars; the metaconule is large, with moderately well developed antero- and posterolabial wings, a few specimens with a crest to the protocone, and in unworn teeth four additional, minor crests on the posterior slope lingual to the posterolabial wing; the tooth is almost surrounded by a highly cuspidate cingulum, the principal interruptions occurring at the bases of the protocone and occasionally the metacone; a hypocone is generally not indicated, but a small cuspule is located in the appropriate position on Calif. Inst. Technology No. 1596 (Stock, 1934b, plate 1, fig. 4.).

Lower jaw with diastemata both anterior and posterior to the roots of $P_2$ (Stock identified these roots as belonging to a single-rooted C and $P_1$, respectively, and was forced by his ideas of hyopsodont affinity to conclude that the posterior diastema was possibly the former site of a $P_2$ lost during life, although he admitted that "no very clear, if any, external indication of the former presence of alveoli can be determined."). Large mental foramen beneath $P_2$; another, small foramen below posterior root of $P_3$. Symphysis extending to beneath posterior root of $P_2$.

$P_2$ double-rooted, strong.

$P_3$ trenchant, typically dichobunid and not closely similar to $P_3$ of hyopsodonts; no crest from protoconid to entoconid and no metaconid (in contrast to *Antiacodon* and *Auxontodon*); main crest to heel as in *Wasatchia, Hexacodus, Leptoreodon, etc.*, in that it seems to stand up as a sharp ridge above the deeply concave posterior face of the protoconid.

$P_4$ elongate, but not as thin and trenchant as $P_3$; paraconid low, distinct, somewhat lingually placed, and with a short cingulum extending basoposterolabially for a short distance; protoconid high, with an anterior crest curving from the apex to the posterolabial base of the paraconid and a sharp ridge running posterobasally from the apex as in $P_3$; metaconid separating from high on protoconid and a weak metastylid developing high on metaconid, creating a sharp groove between itself and the main posterior ridge of the protoconid (The high metaconid differs from that of *Hexacodus, Microsus, Antiacodon,* or *Auxontodon,* the only other American dichobunids exhibiting the cusp on $P_4$. *Antiacodon* and *Microsus* have well separated, low metaconids, evidently derived from the condition seen in *Hexacodus,* in which a weak, low metaconid is developed at the base of the protoconid of a tooth which is otherwise similar to $P_4$ of *Diacodexis* and *Protodichobune*. *Auxontodon* has a high metaconid, but the cusp is well separated and is evidently derived from that of *Antiacodon.*); the metastylid does not extend to the base of the metaconid; entoconid present, though the cusp is generally absent in American dichobunids (present only in *Hexacodus, Antiacodon, Auxontodon,* and weakly in *Diacodexis robustus.*).

$M_1$ with paraconid and metaconid not well separated, in agreement with *Microsus* (Gazin, 1955, p. 23), but in disagreement with *Homacodon,* in which there is a single lingual trigonid cusp, and with *Antiacodon* and *Auxontodon,* in which the paraconid and metaconid are very well separated; paraconid larger than metaconid in agreement with *Auxontodon;* anterior cingulum and parts of labial cingulum heavy in contrast to most members of the Diacodexinae; looping paralophid as in *Homacodon* and *Microsus,* but also similar to that of hyopsodont condylarths; metaconid and hypoconid apices connected by notched metalophid; strong hypoconid connected to hypoconulid as in *Hexacodus* (Gazin, 1952, p. 75).

$M_2$ as in $M_1$ except larger, with paraconid subordinate to metaconid and easily obliterated by wear as in *Microsus* (Gazin, 1955, p. 23); several tiny crenulations on anterior crest of entoconid.

$M_3$ narrower than $M_2$, with paraconid completely engulfed in incomplete paralophid loop as is usually the case in *Microsus* (Gazin, 1955, p. 23); hypoconulid large, but not narrowly projecting as in *Wasatchia, Diacodexis, Homacodon,* etc.; hypoconulid variably connected to other posterior talonid cusps, but most frequently connected to hypoconid; additional crests directly connecting the entoconid to the hypoconid may be present.

DISCUSSION:

Stock (1934b) compared *Tapochoerus egressus* with advanced hyopsodont condylarths but did not mention dichobunid artiodactyls. One is thus led to assume that the dichobunids were overlooked as possible relatives of *Tapochoerus.* Had these additional comparisons been made I believe that Stock would not have placed *Tapochoerus egressus* in the Hyopsodontidae. Certain similarities to *Haplomylus* and *Hyopsodus,* such as looping paralophids and weakly separated paraconids on the lower molars, a metaconid on $P_4$, bunodont crowns, and a small hypocone on the anterior upper molars, also support dichobunid relationships. Considered in detail, the similarity to the dichobunids is always greater. In addition, the presence of diastemata, the placement of the lower molar hypoconulids, and the trenchant nature of the premolars indicate artiodactyl affinities.

Possession of a hypocone is a distinctive feature of *Tapochoerus.* American dichobunids differ from their European counterparts in that the hypocone is either not present (Helohyinae, Diacodexinae, except possibly some specimens of *Bunophorus*) or if so, it is generally reduced in conjunction with progressive hypertrophy of the metaconule (advanced homacodonts). In *Antiacodon,* which together with *Auxontodon* represents a distinctive but minor side branch of the homacodont complex, the hypocone is present on $M^1$ and $M^2$ but the metaconule is not hypertrophied. Although the premolars remove *Antiacodon* from the ancestry of all later homacodonts except *Auxontodon,* the molars probably do not differ greatly from the primitive homacodont condition. *Tapochoerus* is in agreement with *Antiacodon,* in that the metaconule is not hypertrophied. Unfortunately, the upper molars of *Hexacodus* are not yet known.

Lower molars of *Tapochoerus* resemble those of the presumably primitive homacodont genus *Microsus* in the presence of a distinct paraconid on $M_1$, variable paraconid on $M_2$, and loss of the paraconid on $M_3$ (present in some specimens of *Microsus*). Other homacodonts depart widely from this condition. *Homacodon* itself has only one lingual trigonid cusp on each lower molar. In *Antiacodon* the paraconid and metaconid are much more widely separated than in *Tapochoerus*. In the one preserved molar ($M_1$) of *Auxontodon* the paraconid and metaconid are widely separated, but the paraconid is the larger cusp as in *Tapochoerus*.

The lower premolars also ally *Tapochoerus* with the homacodonts. Among American dichobunids, only in members of the Homacodontinae is a metaconid found on $P_4$. Curiously enough, however, *Homacodon* itself lacks the cusp. The $P_4$ metaconid of *Tapochoerus* is more closely appressed to the protoconid than in other homacodonts, but the cusp is variable within the group. Presence of a $P_4$ entoconid also suggests the Homacodontinae, though this cusp is easily acquired phylogenetically, as seems to be the case with *Diacodexis*.

Several minor lineages among the homacodonts do not lead toward *Tapochoerus*. *Homacodon* itself has already lost one of the lingual trigonid cusps of the lower molars, lacks a metaconid on $P_4$, and already shows hypertrophy of the metaconule of the upper molars, notably $M^3$. *Homacodon* was already too advanced to have given rise to *Tapochoerus*. *Antiacodon* and its probable descendant, *Auxontodon*, possess highly characteristic $P_3$ and $P_4$, each tooth bearing a metaconid. This cusp is unknown in $P_3$ of other American dichobunids and gives $P_3$ a distinctive "triconodont" aspect in this lineage. The lineage apparently arose from a *Hexacodus*-like primitive homacodont stock during the Wasatchian and carried on to the late Uintan genus *Auxontodon*. Gazin (1958, p. 2) created a new subfamily, Antiacodontinae, for the two genera, but the two forms are closely similar to each other in comparable details and together are not more distinctive than other vertical branches of the homacodonts (e.g., *Homacodon* itself or *Mesomeryx*), though the inferred caniniform $P_1$ of *Auxontodon* was considered important by Gazin. *Bunomeryx*, a Uintan homacodont, possesses an enlarged $P_1$ (Peterson, 1919a, p. 67). This part of the jaw is almost completely unknown in middle and early Eocene homacodonts. The distribution of enlarged and presumably caniniform first premolars within the homacodonts is therefore too poorly understood for taxonomic use at present. At this time, therefore, recognition of the antiacodont lineage as a distinct subfamily does not seem to me to be justified. While distinct, the antiacodonts are just one minor lineage within a complex of equally distinctive lineages, all of which fit conveniently into one useful subfamily, the Homacodontinae.

*Tapochoerus* appears to be related to the primitive homacodonts and on the basis of available evidence is closely related especially to *Hexacodus* and *Microsus*. Four homacodont lineages therefore existed during the middle Eocene in North

America: *Homacodon* itself, leaving no known descendants; *Antiacodon*, leading to the late Eocene *Auxontodon; Microsus*, leading to advanced late Eocene homacodonts; and the ancestry of *Tapochoerus*, presumably restricted to the West Coast and undergoing little significant modification from the early Eocene onward.

Measurements (mm.)

| | |
|---|---|
| ?$M^2$ (C.I.T. No. 1598) ectoloph length: maximum width | 7.7 : 9.3 |
| $M^3$ ectoloph length: maximum width | 6.0-6.4 : 7.4-7.8 |
| Depth of lower jaw (C.I.T. No. 1292) at diastema between $P_1$ and $P_2$ | est. 9.0 |
| Depth of lower jaw beneath $M_2$, lingually | 12.5-13.2 (10.6 in one young adult) |
| Length of diastema (C.I.T. No. 1292) between $P_1$ and $P_2$ | est. 4.0 |
| Length of cheek tooth series from anterior margin of first alveolus of $P_2$ to posterior margin of $M_3$ | est. 50.0 |
| Length of lower molar series, $M_1$-$M_3$, inclusive | 22.5-est. 23.0 |
| $P_3$, length: greatest width (C.I.T. No. 1292) | 7.4 : 3.2 |
| $P_4$, length: greatest width (C.I.T. No. 1292) | 8.3-8.8 : 4.0-4.8 |
| $M_1$, length: greatest width (C.I.T. No. 1292) | 7.1-7.3 : 4.7-4.9 |
| $M_2$, length: greatest width (C.I.T. No. 1292) | 7.4-8.0 : 5.1-5.3 |
| $M_3$, length: greatest width (C.I.T. No. 1292) | 7.3-7.9 : 4.5-5.1 |

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